

1 **LONG-TERM CHANGES IN POPULATION SIZE, DISTRIBUTION AND PRODUCTIVITY**
2 **OF SKUAS (*Stercorarius* spp.) AT SIGNY ISLAND, SOUTH ORKNEY ISLANDS**

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21 Abstract

22 In this study, we investigate the numbers, productivity and territory distribution of the two
23 species of skuas (brown *Stercorarius lonnbergi* and south polar *Stercorarius maccormicki*)
24 breeding at Signy Island, South Orkneys, and compare the results with trends elsewhere.
25 Comparison with previous counts indicates a biphasic increase in brown skuas at Signy
26 Island; much faster from 1958/59 to 1982/83 (3.3% per annum), than in subsequent years
27 (0.4% per annum from 1983/84 to 2013/14). Relative distribution of territories has changed
28 little over time. The reduced rate of population growth in recent years was broadly coincident
29 with a decrease in numbers of penguins (and therefore potential prey), which may also
30 explain recent reductions in skua numbers at other Antarctic sites. As prey have become
31 limiting, breeding success of brown skuas at Signy Island is now slightly lower than in the
32 1950s/early 1960s, but timing of breeding does not appear to have changed. Brown skuas at
33 Signy Island may still have enough resources to start breeding, but as the season
34 progresses and availability of resources declines, chick survival is reduced. South polar
35 skuas have declined from 10 pairs in 1982/83 to one pair in 2013/14, and mixed-pairs have
36 increased from one to three pairs. A review of the literature indicated that although
37 population trend data are available for relatively few sites elsewhere in the subantarctic and
38 Antarctic, numbers of brown skuas appear to be generally decreasing or stable, and of south
39 polar skuas to be stable or increasing.

40 Keywords: Breeding success; Population trends; Seabird; *Stercorarius* spp.; Top predator

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45 Introduction

46 Seabirds are top predators in marine ecosystems and often considered to be effective
47 monitors of the condition and health of aquatic systems (Furness and Camphuysen 1997).
48 Particularly in the Southern Ocean, there is increasing evidence that the population
49 dynamics of top predators have been subjected to the compounded effects of human
50 activities (including harvesting, pollution, introductions of alien species etc.) and global
51 climate change; the latter has led in some cases to changes in phenology across multiple
52 trophic levels and a mismatch between peak energy demands of predators and the
53 availability of their key prey (Jenouvrier et al. 2005; Österblom et al. 2006; Ainley and
54 Hyrenbach 2010; Péron et al. 2010; Péron et al. 2013). Accurate knowledge of the
55 distribution and abundance of marine predators can therefore provide insights into
56 ecosystem status, as well as essential information for management and conservation
57 (Creuwels et al. 2007; Chardine et al. 2013).

58 Skuas *Stercorarius* spp. are important top predators in Antarctic environments.
59 Together with giant petrels (*Macronectes* spp.), skuas are the only avian predators likely to
60 have a major impact on populations of other seabirds (Norman and Ward 1990). Brown
61 skuas (*S. lonnbergi*) breed on most sub-Antarctic islands and in the Chatham Islands, south
62 polar skuas (*S. maccormicki*) breed at high latitudes around the Antarctic continent, and the
63 two species overlap in the northern parts of the Antarctic peninsula (Furness 1987; Fig. 1).
64 Both species are regarded as opportunistic predators, scavengers and kleptoparasites,
65 which enables them to exploit a wide range of food resources (Moncorps et al. 1998;
66 Mougeot et al. 1998; Phillips et al. 2004; Malzof and Quintana 2008; Carneiro et al. 2014). In
67 southerly regions, brown skuas feed mainly on penguin and other seabird prey, as do south
68 polar skuas throughout most of their breeding range, but in areas of sympatry, the latter
69 species forages almost exclusively at sea (Trivelpiece et al. 1980; Pietz 1987; Reinhardt et
70 al. 2000).

71 Results from the few long-term studies of brown and south polar skuas indicate
72 considerable variation in population trends among sites; mostly decreasing or stable for
73 brown skuas, but stable or increasing for south polar skuas until the 1990s (Woehler et al.
74 2001; Phillips et al. 2004). The hybrid zone between the two species expanded with a
75 northerly extension of the south polar skua range in the late 1970s (Ritz et al. 2006). At
76 Signy Island, South Orkneys, the breeding population of brown skuas doubled between
77 1958/59 and 1982/83 (Burton 1968; Hemmings 1984; Rootes 1988), and a new population
78 of south polar skuas was established in 1978/79 (Hemmings 1984).

79 Increases in skua numbers have been attributed to a rapid growth in penguin
80 numbers (and therefore potential prey) since the 1950s, or availability of seal carrion (Rootes
81 1988; Phillips et al. 2004). In recent years, however, penguin populations at Signy Island
82 have declined, considered to be a consequence of reduced prey biomass and increased
83 competition for resources, associated with changes in the timing and extent of sea ice
84 formation, and the recovery of seal and whale populations (Forcada et al. 2006). The aim of
85 this study was to document possible responses of brown and south polar skuas breeding at
86 Signy Island to changes in the availability of penguins (as prey) in the 30+ years since the
87 last census. In addition, territory distribution, nesting density, and breeding parameters
88 (timing, breeding success) are compared with previously published data from this site and
89 elsewhere.

90

91 Materials and methods

92 Territories of breeding skuas (mostly brown skuas, but including a few pairs of south polar
93 skuas and a mixed-species pair) were studied at Signy Island, South Orkney Islands (60°43'
94 S, 45°36' W; Fig. 2), between late December (mid incubation) and early March (chick
95 fledging) in the austral summer of 2013/14. All individuals were identified to species level by

96 plumage coloration, differences in body size and vocalisations. A full census of the island
97 was carried out by visiting all ice-free areas and recording the position of nests with eggs,
98 and defended territories without eggs, using a hand-held GPS logger. The majority of
99 territories with eggs (~79%) were checked at 5-8 day intervals during the breeding season,
100 and the remainder were visited at least twice (in incubation and late chick-rearing). Wing
101 length (maximum flattened chord) and mass of the chicks were measured at each visit
102 during chick-rearing. Hatching dates were observed directly or estimated using a logistic
103 curve fitted to the relationship between wing length and age of chicks of known hatching
104 date (Phillips et al. 2004) using the function `nls` in R. To ensure statistical independence,
105 comparisons of hatching date were based on the first chick hatched in each clutch. Overall
106 breeding success was calculated for each type of skua pair (brown, south polar, or mixed) as
107 the number of chicks fledged per clutch laid. Chicks were assumed to have fledged if they
108 survived to >50 days, or until the end of the study period, as the mortality rate of older chicks
109 is low (Hahn and Peter 2003).

110 Population size, territory distribution and breeding parameters (timing, breeding success) in
111 2013/14 were compared with data from part or the whole island available for previous years
112 in published papers and unpublished reports (Richards 1958; Pinder 1960; Jones and Pinder
113 1961; Topliffe 1962; Burton 1968; Hemmings 1982, 1984; Rootes 1988). Nesting density
114 (pairs per km²) was calculated according to: (1) the planar area of the entire island, and, (2)
115 the planar area of suitable habitat, which excluded slopes above 150 m, and cliffs (Phillips et
116 al. 2004). Minimum distances between neighbouring territories were also estimated from the
117 GPS data.

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119 Results

120 The number of skua pairs breeding at Signy Island has been counted sporadically since
121 1958/59 (Table 1). Although skua numbers have changed substantially over time, the
122 relative distribution of nests in 2013/14 is similar to that recorded in 1958/59, 1965/66 and
123 1982/83 (Fig. 2). Territories of brown skuas occur throughout the island, with the greatest
124 densities around the penguin colonies, and have always been scarce at higher elevations
125 (Fig. 2). The majority of nests of south polar skua and mixed-species pairs remain clustered
126 in the far south-east of Signy Island, which is the area where south polar skuas were
127 breeding in 1982/83 (Fig. 2). The skua nesting density in 2013/14 was nine pairs per km²
128 over the entire island (18.9 km²), and 15 pairs per km² over the area of suitable habitat (10.7
129 km²). Minimum distance from each territory to its nearest neighbour ranged from 15.6 to
130 457.5 m (mean \pm se, 103.6 \pm 6.4 m). The majority of territories (60.6%) were <100 m apart,
131 and very few (3.0%) were >300 m from the nearest neighbour.

132 In total, 165 occupied territories (including five in which breeding was not confirmed)
133 were counted on Signy Island during 2013/14. Of these, 161 were defended by a pair of
134 brown skuas, one by a pair of south polar skuas, and three by mixed pairs (Table 1). Counts
135 of occupied territories were available for part or the entire island in previous seasons,
136 including most years from 1958/59 to 1965/66, and 1982/83 (Table 1). In seasons between
137 1958/59 to 1965/66 in which only part of the island was surveyed, the population size of
138 brown skuas for the whole island was estimated based on the proportion of territories in
139 these areas relative to those elsewhere on the island in 1960/61 (Pinder 1960; Hemmings
140 1982). The long-term trend in the breeding population of brown skuas appears to be
141 represented by two major phases; a relatively rapid increase from 1958/59 to 1982/83 (3.3%
142 per annum), and a much slower increase in subsequent years (0.4% per annum from
143 1982/83 to 2013/14), equivalent to a 1.7% increase per annum overall. The breeding
144 population of south polar skuas has declined from 10 pairs in 1982/83 to only one pair in
145 2013/14, and of mixed-pairs has increased from one to three pairs (Table 1).

146 The number of chicks fledged per pair of brown skua in the 2013/14 season was 0.97
147 (N= 150), and per mixed-pair was 1.33 (N= 3); the pair of south polar skuas failed to fledge
148 any chick. The productivity of brown skuas in 2013/14 was slightly lower than in any of the
149 seven years from 1958/59 to 1965/66 (range 1.06 to 1.42 chicks/pair) for which data are
150 available (Table 1).

151

152 Discussion

153 The brown skua population at Signy Island increased by 3.3% per annum from the first
154 survey in 1958/59 to 1982/83, and by 0.4% per annum in the subsequent 31 years to the
155 present study (for references see Tables 1 and 2). This represents an overall annual
156 increase of 1.7% per annum over the 55 years since the first count. In contrast, the
157 population of south polar skuas increased after colonisation by two pairs in 1978/79 to 10
158 pairs in 1982/83, but had decreased to just one pair in our recent survey; over the same
159 period, the number of mixed-species pairs has increased from one to three pairs (Tables 1
160 and 2). The decline in south polar skuas may have been driven by the increase in brown
161 skuas, which are considerably larger and are better competitors on land, or it may reflect
162 reduced abundance of the Antarctic silverfish (*Pleuragramma antarcticum*). This was the
163 main component of the diet of south polar skuas in the early 1980s and may have facilitated
164 their original expansion in range to Signy Island (Hemmings 1984). The south polar skuas in
165 the mixed pairs probably represent the surviving members of these original colonists, or their
166 offspring.

167 Skua population trend data are available for relatively few sites (Table 2, Fig. 1).
168 Although these trends are highly variable and there are few data for recent years, numbers
169 of brown skuas appear to be generally decreasing or stable, and of south polar skuas to be
170 stable or increasing, although there are exceptions (Table 2). Brown skua breeding numbers

171 were stable at the Kerguelen and Chatham archipelagos, and Anvers Island; stable or
172 declining (although with substantial annual fluctuations) at different sites on King George
173 Island (South Shetlands), stable at Macquarie Island, and Marion Island (Prince Edward
174 Islands), and increasing substantially at Bird Island (South Georgia), and at Prince Edward
175 Island. Populations of south polar skuas were stable at different sites on Ross Island;
176 increased at sites in King George Island (although recent counts indicate declines) and
177 elsewhere in the South Shetlands, and at Adélie Land, and Anvers Island. The more limited
178 data for mixed-species pairs indicate stable or increasing trends. See Table 2 for references
179 and a more detailed comparison.

180 The biphasic increase in the population of brown skuas has occurred in parallel with
181 changes in population sizes of pygoscelid penguins (chinstrap *Pygoscelis antarctica* and
182 Adélie *P. adeliae*) at Signy Island over the same time period. Adélie and chinstrap numbers
183 increased up to fivefold from the 1950s to the mid 1970s at breeding colonies in the Scotia
184 Sea, attributed to competitive release following the cessation of commercial harvesting of
185 whales and seals (Croxall et al. 1981; Trivelpiece et al. 2011). The subsequent decline is
186 considered to have resulted from the reduction in prey biomass (Antarctic krill *Euphausia*
187 *superba*) due to climate change (through reduction in winter sea-ice extent), and the
188 recovery of seal and whale populations (Forcada et al. 2006; Hinke et al. 2007; Sander et al.
189 2007a,b; Carlini et al. 2009; Trivelpiece et al. 2011; Barbosa et al. 2012). One possible
190 explanation for the slowing of skua population growth rate at Signy Island is that the
191 availability of penguins as prey has become limiting. This is supported by the slightly lower
192 breeding success in 2013/14 when compared with the late 1950s and early 1960s (Table 1).
193 This seems to reflect the increased use of other resources in addition to penguin prey;
194 regurgitates collected from brown skuas in 1981/82 and 1982/83 at Signy Island contained
195 only avian material (Hemmings 1984), whereas the analysis of GPS tracking data collected
196 during the breeding season of 2013/14 indicates that skuas now use three different foraging

197 strategies, exploiting penguin colonies, small petrels and marine resources (authors'
198 unpublished data).

199 Although diet seems to have diversified in response to declining resources, timing of
200 breeding on Signy Island does not appear to have changed since the 1950s/early 1960s;
201 mean hatching dates in 1963/64-1965/66, 1982/83 and 2013/14 were all in the first week of
202 January (Richards 1958; Burton 1968; Hemmings 1984; this study), and were similar to
203 those recorded for brown skuas at King George Island in 1983/84 to 2003/04, and at South
204 Georgia in 2000/01 and 2002/03 (Hahn and Peter 2003; Phillips et al. 2004; Hahn et al.
205 2007). Although some brown skuas at Signy Island occupy feeding territories in penguin
206 colonies, which can sustain skuas for much of the season (Hahn and Peter 2003; Hahn and
207 Bauer 2008), other birds at Signy Island feed in penguin colonies that are not defended
208 consistently by another pair of skuas, or elsewhere on small petrels and marine prey (see
209 above). It is possible that these non-territorial skuas have enough access to food, including
210 penguins, to start breeding, but as the season progresses and availability of resources
211 decreases, they may fledge fewer chicks because they have to rely on alternative and less
212 temporally and spatially predictable prey (Trivelpiece et al. 1980; Pietz 1986, 1987; Votier et
213 al. 2004). This would explain the slight decline in breeding success from the 1950s/early
214 1960s to the present. However, even if this somewhat reduced breeding success is the
215 result of density-dependent competition for resources, it is important to note that productivity
216 of brown skuas at Signy Island remains similar to levels reported for populations breeding
217 elsewhere (0.5-1.8 chicks fledged/pair) (Reinhardt 1997; Phillips et al. 2004; Hahn et al.
218 2007). There is no evidence of any substantive long-term change in breeding chronology of
219 penguins at Signy Island (Lishman 1985; British Antarctic Survey unpublished data).

220 Phillips et al. (2004) pointed out that habitat saturation (in terms of feeding or nesting
221 resource availability) can also restrict recruitment rates in skuas. It is difficult to make a direct
222 comparison of nesting densities at Signy Island with skuas breeding elsewhere because of

223 the considerable variation in prey availability and the variety of skua foraging strategies.
224 However, when comparing with sites where the main food resources on land are penguin
225 eggs and chicks, as on Signy Island, nesting densities are in general similar. The overall
226 density across Signy Island is 15 pairs per km², which is comparable with that at King
227 George Island, South Shetland Islands (15.3 pairs per km² in 2004/05; Carneiro et al. 2010).
228 Part of the skua population that usually breeds at King George Island, however, deferred
229 breeding in the last three consecutive seasons (Carneiro et al. 2015; Trivelpiece pers.
230 comm.), indicating that a nesting density of about 15 birds per km² may represent the
231 threshold that limits the establishment of new territories. It is possible that the skua
232 population at Signy Island reached close to the maximum sustainable at some point during
233 the 1980s, hence the subsequent reduction in growth rate and decreased breeding success.
234 In contrast, at Bird Island (South Georgia) where brown skuas feed mainly by scavenging
235 seal carrion and placentae on beaches, and to a lesser extent by predation of other
236 seabirds, the nesting density in the austral summer of 2003/04 was far higher, at 119 pairs
237 per km², and the minimum nest spacing just 44 m, on average (Phillips et al. 2004). Bird
238 Island is, however, by far the most densely populated colony of brown skuas in the world
239 with comparatively good feeding conditions related to the abundance of fur seal carrion
240 (Phillips et al. 2004; Anderson et al. 2009).

241 In conclusion, it seems unlikely that breeding numbers on Signy Island will increase
242 to any great extent in the future because of a combination of decreased penguin abundance
243 and habitat saturation. Future work should involve monitoring of skua numbers and breeding
244 success at Signy Island and elsewhere in order to assess the conservation status of these
245 species. Both the brown skua and south polar skua remain relatively uncommon seabirds in
246 global terms, with a worldwide population of just c. 7–9,000 and 8–10,000 breeding pairs,
247 respectively, of which an estimated 3-4% and <1% breed in the South Orkney Islands
248 (Furness 1987; Higgins and Davis 1996). Indeed, this study stresses the importance of long-
249 term population monitoring programs in general, especially for species that are subject to

250 strong annual fluctuations such as skuas, to detect trends more reliably and to identify their
251 underlying causes.

252

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428 Table 1: Long-term changes in population size and breeding success of brown skuas
429 (*Stercorarius lonnbergi*), south polar skuas (*S. maccormicki*) and mixed-species pairs at
430 Signy Island.

| Season | Count of occupied territories | | | Brown skua productivity (chicks fledged/pair) | Reference |
|----------------------|-------------------------------|---------------------|----------------|---|----------------------------------|
| | Brown skua | South polar skua | Mixed pairs | | |
| 1958/59 ^a | 65 | 0 | 0 | 1.30 | Richards (1958) |
| 1960/61 | 71 | 0 | 0 | 1.30 | Pinder (1960); Hemmings (1982) |
| 1961/62 | 81 | 0 | 0 | 1.16 | Jones and Pinder (1961) |
| 1962/63 | 64 | 0 | 0 | 1.42 | Topliffe (1962); Hemmings (1982) |
| 1963/64 ^b | 79 | 0 | 0 | 1.32 | Burton (1968) |
| 1964/65 ^c | 99 | 0 | 0 | 1.10 | Burton (1968) |
| 1965/66 ^d | 96 | 0 | 0 | 1.06 | Burton (1968) |
| 1981/82 | NA | 9 | 3 | NA | Hemmings (1984) |
| 1982/83 | 143 | 10 | 1 | NA | Hemmings (1984) |
| 2013/14 | 161 | 1 | 3 | 0.97 | This study |

Estimate based on original part-island counts (of ^a59, ^b67, ^c84 and ^d81 pairs), corrected for the proportion of territories in surveyed and unsurveyed areas recorded in 1960/61.

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438 Table 2: Trends in population sizes of brown skuas (*Stercorarius lonnbergi* - BS), south polar skuas (*S. maccormicki* - SPS) and mixed-species pairs (MS). ^a

439 Most recent count. See Fig. 1 for the location of study sites.

| Site | Study period | Species | Occupied territories ^a | Trend | Reference |
|--------------------------|------------------------|---------|-----------------------------------|------------|------------------------|
| 1. Chatham Islands | | | | | |
| Mangere Island | 1980-1992 | BS | 19 | Stable | Young (1994) |
| Rangatira Island | 1979-1992 | BS | 43 | Stable | Young (1994) |
| 2. Prince Edward Islands | | | | | |
| Prince Edward Island | 2001, 2008 | BS | 267 | Increasing | Ryan et al. (2009) |
| Marion Island | 1987, 1997, 2001, 2008 | BS | 282 | -5% | Ryan et al. (2009) |
| 3. Iles Kerguelen | | | | | |
| Ile Verte | 1991-2006 | BS | 6 ± 1 (average) | Stable | Brodier et al. (2011) |
| 4. South Georgia | | | | | |
| Bird Island | 1958, 1976, 1980 | BS | 375 | +3.6% | Phillips et al. (2004) |
| | 1981-2003 | BS | 467 | +0.9% | |
| 5. Macquarie Island | 1974, 1983 | BS | 206 | Decreasing | Skira (1984) |
| 6. South Orkney Islands | | | | | |
| Signy Island | 1958, 1960-1965, 1982 | BS | 143 | +3.3% | This study |
| | 1983-2013 | BS | 161 | +0.4% | |

| | | | | |
|-------------------|------------------|-----|-----|------------|
| | | MS | 16 | Stable |
| | 2012, 2013 | BS | 14 | Decreasing |
| | | SPS | 0 | Decreasing |
| Livingston Island | | | | |
| Byers Peninsula | 1965, 2008 | BS | 15 | Decreasing |
| Half-moon Island | 1993, 1994, 1995 | BS | 3 | Stable |
| | 1993, 1994, 1995 | SPS | 103 | Stable |

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446 Figure captions:

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448 **Fig. 1** Breeding distribution of brown (*Stercorarius lonnbergi*) and south polar skuas (*S.*
449 *maccormicki*). Filled symbols represent sites with at least two years of count data (see Table
450 2); open symbols indicate that no trend was available. Site names (1-11: see Table 2, 12:
451 Iles Crozet, 13: Amsterdam and St Paul, 14: Heard and McDonald Islands, 15: New Zealand
452 and offshore islands, 16: The Snares, 17: Auckland Islands, 18: Campbell Islands, 19:
453 Antipodes Islands, 20: Bounty Islands, 21: South Sandwich Islands, 22: Bouvet Island, 23:
454 Peter I Island, 24: Antarctic coast and offshore islands)

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456 **Fig. 2** Location and maps of the study site. (a) South Orkney Islands. Distribution of nests
457 and occupied territories of brown skuas (*Stercorarius lonnbergi*), south polar skuas (*S.*
458 *maccormicki*) and mixed-species pairs at Signy Island (South Orkneys) in (b) 1958/59
459 (redrawn from Richards 1958), (c) 1965/66 (redrawn from Burton 1968), (d) 1982/83
460 (redrawn from Rootes 1988), and (e) 2013/14

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Fig. 1.

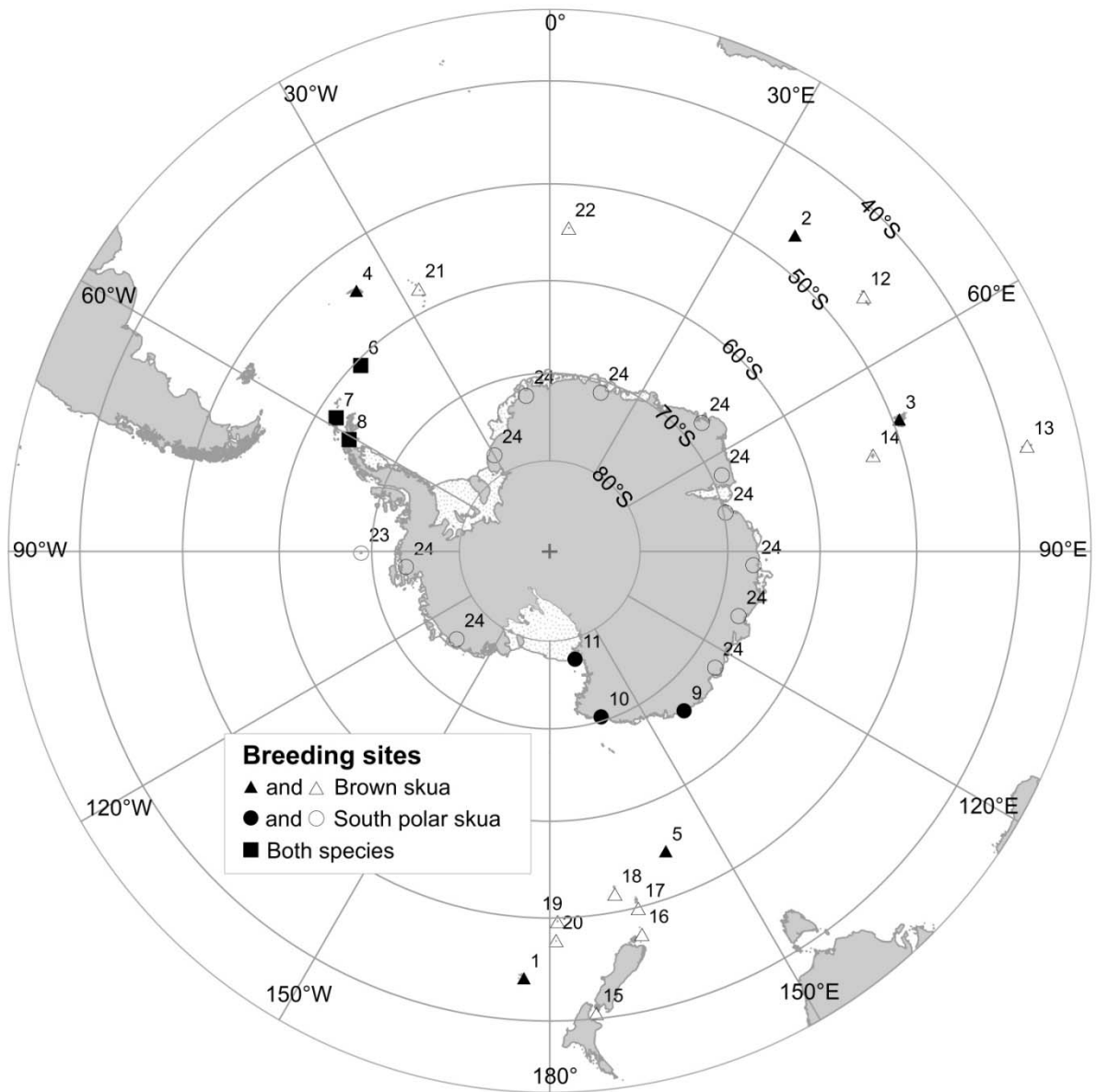


Fig. 2.

